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Note on the sexual generation and the development of the seed-coats in certain of the Papaveraceae

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(WITH PLATE 15)

During the past two years the writer has mounted and examined material in some quantity of *Sanguinaria*, *Chelidonium* and *Eschscholtzia*. The facts in hand indicate that the embryo-sac phenomena do not widely depart from those described, for instance, in genera of the *Ranunculaceae*. The following are some of the facts observed.

Annual phases of Sanguinaria.—Material of *Sanguinaria* has been gathered at various seasons in order to obtain a complete view of the annual life-cycle. The flowers of the plant begin to be formed nearly a year before they appear, viz., in May of the preceding year, while the seeds of that season are becoming mature. The stamens develop more rapidly than the carpels. By August the anthers are well formed, with four-lobed outline in cross-section, and the sporogenous tissue is beginning to be differentiated from that of the anther-walls. Cell-division proceeds during autumn, the size of the anther as a whole meanwhile increasing. The cells lying toward the periphery of the sporogenous mass begin to degenerate and by November the spore-mother-cells are seen as richly filled cells lying among the more or less disorganized tapetal cells. In this condition the winter is passed. Division of the mother-cells begins very early in the spring. Material killed on February 4, 1903, after several days of very mild weather, shows figures of dividing nuclei. Development of the spores and the final formation of the anther-wall seem, as might be expected, to be somewhat controlled by the weather, but are completed during this period, between the renewal of growth and blooming. The ovules begin to appear about August as undifferentiated outgrowths of the placental tract, but development lags behind that of the anthers. The integuments are not developed till the close of winter, at the time when the microspores are being formed from their mother-cells. No trace of the megaspore mother-cell is visible when growth is renewed in late winter. *Sanguinaria* is therefore in this respect like *Salix* and *Populus*, whereas certain other plants, most definitely *Epigaea* and *Erythronium*, have been observed to reach the mother-cell stage during the preceding season.

The division of the megaspore mother-cells and the formation of the embryo-sac take place during March and early April. Although the development of the microspores has kept far in advance, the flower at blooming is proterogynous. As is well known, the phases from pollination to maturity of seeds occur in April, May and June.

Structure of the pistil.—In *Sanguinaria*, *Chelidonium* and *Eschscholtzia*, an open canal leads from the ovary to the exterior. Hairy outgrowths of a kind with those of the stigma project into the passage but generally do not close it, and continue down the two placental ridges. Thus the hairy outgrowths of the stigma, of the interior of the stylar canal and of the placental ridges form a single continuous tract. This is highly developed in *Sanguinaria*, less so in *Chelidonium* and *Eschscholtzia*, but distinctly in all. The path of the pollen-tubes is among these hairs and the loose superficial cell-layers from which they spring. The tubes pass through the micropyle and penetrate the nucellus in the usual manner.

The embryo-sac.—The embryo-sac exhibits the typical number and arrangement of nuclei (PLATE 15, FIGURES 1 AND 2). The polar nuclei are often met with, lying close together. In the antipodal region are found features of interest. The antipodal cells reach an unusual size, and the nucellar cells in their vicinity acquire thickened walls. In *Eschscholtzia* the antipodals continue to enlarge for a brief period during the early formation of the endosperm nuclei and then decrease and disappear before the endosperm cells are cut out.

In *Chelidonium* (PLATE 15, FIGURE 2), the antipodals are relatively smaller than in *Eschscholtzia* but they persist longer and may be seen after walls have formed about the endosperm cells. For *Sanguinaria* also the statements in regard to *Chelidonium* hold true.

In all three forms the cells in the nucellus adjacent to the antipodals acquire thickened walls (PLATE 15, FIGURE 1). This tissue increases during the enlargement of the sac and the formation of the endosperm. It can scarcely be doubted that to this tract, together with the enlarged antipodals, some nutritive significance attaches.

The size of the nucleoli is noteworthy both in the nuclei of the embryo-sac and those of the surrounding cells. Practically all of the strongly staining substance of the nuclei is included in them. It is difficult to entertain any other idea than that these nucleoli embrace the chromatin.

DEVELOPMENT OF THE SEED-COATS IN SANGUINARIA

The integuments arise shortly after renewal of growth in the spring as two folds growing up around the nucellus. Each consists throughout most of its extent of three cell-layers (PLATE 15, FIGURE 3). Following is a description of the differentiation and destiny of each of these:

(*a*) *The secundine.*—The inner of the three cell-layers undergoes anticlinal division as the ovule enlarges, so that at the time when the egg-apparatus is formed the cells are still nearly isodiametric (PLATE 15, FIGURE 4). At this time they have the appearance of active cells with abundant protoplasm and well-developed nuclei. Very soon, however, their anticlinal division becomes less active and at the same time they are stretched by the expanding embryo-sac. By the time that the endosperm nuclei have spread to the wall of the embryo-sac this layer is losing its organization, and thereafter appears only as an ill-defined rudiment (PLATE 15, FIGURES 5 AND 6).

The middle layer of the secundine has almost from the first less protoplasmic contents. At the time of the completion of the egg-apparatus it appears highly vacuolated with larger cells and degenerating nuclei. This is the first of all the layers to break down, the cells losing their form shortly after fertilization.

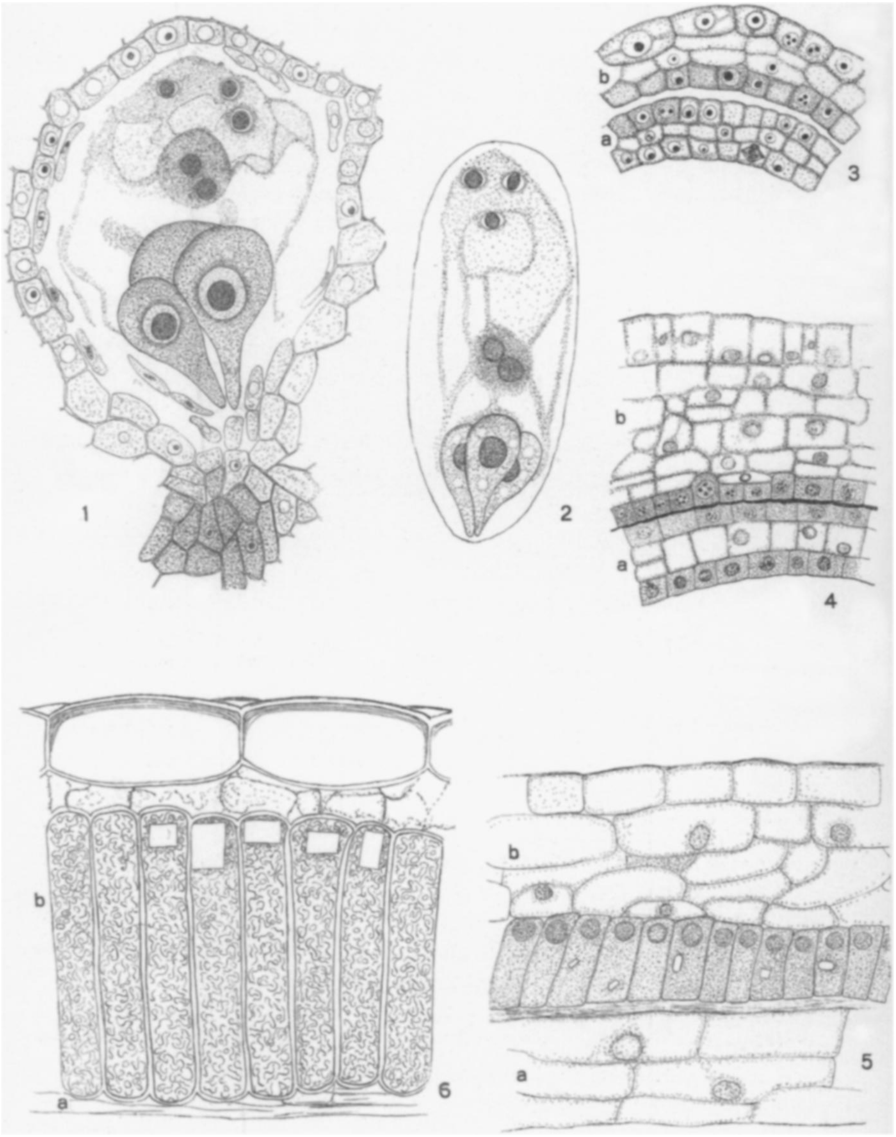
The outer layer of the secundine does not become vacuolated to so great a degree as the one last named and it persists somewhat longer. But it shares the fate of the other layers of the secundine, appearing while the endosperm is forming only as a mass of distorted and fragmentary cell-bodies.

(*b*) *The primine.*—The persistent parts of the seed-coats are formed exclusively from this tissue. The inner layer is marked almost from the first by its richer contents of protoplasm and active nuclei (PLATE 15, FIGURE 3). Anticlinal division nearly or quite keeps pace with the swelling of the ovule, so that at the time of the completion of the egg-apparatus (PLATE 15, FIGURE 4) the cells are nearly or quite isodiametric. Shortly after that period a great anticlinal elongation takes place and this layer becomes the first in prominence as it is destined to be in importance of all the cell-layers (PLATE 15, FIGURE 5). From an early date a sort of cuticular layer is formed on its inner surface where it comes in contact with the secundine (PLATE 15, FIGURE 5). The cells continue to be well filled with protoplasm and to have prominent nuclei. About the time when endosperm cells begin to be cut out, crystals of calcium oxalate appear within this layer, and these later accumulate to a considerable degree. While the endosperm is maturing, their layer still further increases in size and becomes greatly indurated. It forms the most important part of the testa, exceeding in thickness all the other layers together (PLATE 15, FIGURE 6).

The middle layer of the primine undergoes both periclinal and anticlinal division so that in the later stages it is several cells deep (PLATE 15, FIGURES 4, 5, 6). All these cells become highly vacuolated, increase in size, and toward the last become compressed by the enlarging inner layer of the primine and almost disappear.

The outer layer of the primine undergoes comparatively few divisions and these are all anticlinal. Although the cells become much enlarged, they are not distorted by pressure nor in any way disorganized, and developing thick walls on every side, they constitute the outer hard and shining coat of the seed (PLATE 15, FIGURE 6). The caruncle arises just outside the vascular tissue of the raphe, and its enormous cells are thin-walled, but by no means poor in contents. Despite the ready ecological explanations advanced, the significance of this caruncle is still, to the writer at least, a mystery.

In *Eschscholtzia* the development of the integuments resembles that in *Sanguinaria*, but with the difference that the principal layer of the testa is composed of smaller cells which have relatively little induration.



EMBRYO-SAC OF ESCHSCHOLTZIA AND CHELIDONIUM
SEED-COATS OF SANGUINARIA

In *Chelidonium*, however, a more considerable difference exists. Both primine and secundine persist and take part in the formation of the seed-coat. In fact the outer cell-layer of the secundine is rather the most indurated of the four or five cell-layers which give protection to the endosperm.

SUMMARY

In *Sanguinaria* the microspore mother-cells are formed during the season preceding blooming, but their division and the formation of the ovular integuments and of the embryo-sac occur after renewal of growth in the spring, just before blooming.

In *Sanguinaria*, *Chelidonium* and *Eschscholtzia* an open canal extends from the carpellary cavity to the exterior.

In the above-mentioned forms the antipodal cells are very prominent, especially so in *Eschscholtzia*, and the adjacent nucellar cells are thick-walled and rich in contents.

In *Sanguinaria* and *Eschscholtzia* the secundine eventually disappears and the inner cell-layer of the primine constitutes the most important element of the testa. In *Chelidonium* both primine and secundine persist and take part in the formation of the seed-coat.

Explanation of plate 15

All drawings were made with camera lucida. Figures 3, 4, 5 and 6 are drawn to the same scale.

FIG. 1. Embryo-sac of *Eschscholtzia*.

FIG. 2. Embryo-sac of *Chelidonium*.

FIG. 3. Section through the integuments of *Sanguinaria*, immediately after their formation; *a*, secundine, *b*, primine.

FIG. 4. The same at the time of completion of egg-apparatus. The middle layer of the primine has undergone division.

FIG. 5. The same at the time when endosperm cells are being cut out. The secundine is breaking down.

FIG. 6. The same at maturity of seed, showing the inner layer of the primine greatly enlarged and indurated and containing crystals of calcium oxalate.